OMNIVORY AS A STABILIZING FEATURE
OF NATURAL COMMUNITIES

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Abstract.—Omnivory—defined broadly as feeding on more than one trophic level—occupies a prominent position in discussions of food web architecture and dynamics, due in large part to an enduring conflict regarding omnivory's role in community dynamics. According to classical results from mathematical food web theory, omnivory destabilizes ecological communities, whereas more recent conceptual syntheses suggest that omnivory should be a strongly stabilizing factor in food webs. Working with an arthropod assemblage at Mount Saint Helens, I experimentally addressed this controversy using a two-way factorial design that crossed a manipulation of the degree of omnivory with another ''disturbance'' manipulation that targeted a specific component of the assemblage. In this statistical design, significant interaction effects (i.e., how the community impacts of the disturbance varied with the degree of omnivory) identified key stabilizing or destabilizing influences of omnivory. Overall, my experimental results indicated that increasing the degree of omnivory stabilized community dynamics, in keeping with recent conceptual syntheses.

In classical analyses, the mathematical stability of food webs depends on species richness, web connectance, and linkage strength (May 1973; Paine 1980). Food web models predict that omnivory—defined broadly as feeding on more than one trophic level (Pimm 1982; Menge and Sutherland 1987; Sprules and Bowerman 1988; Power 1990; Polis 1994)—destabilizes ecological communities (Pimm and Lawton 1978; Pimm 1982; Pimm et al. 1993). However, recent empirical syntheses (Strong 1992; Polis and Strong 1996) indicate that extensive omnivory could be a strongly stabilizing factor in reticulate food webs. Despite omnivory's importance as a chief source of complexity in ecological food webs (e.g., Winemiller 1990; Hall and Rafaelli 1991; Polis 1991), its effects on community stability have not been tested experimentally. Here I report results from a field experiment specifically designed to assess the impact of omnivory on the stability of a natural arthropod community. In contrast to the predictions of classical food web models, my experiment suggests that omnivory can be a strongly stabilizing force.

In my analyses I define community stability as the capacity to recover from

an external perturbation (i.e., a short-term ''shock'' to the system) and quantify the community's responses in units of species' densities and species' rates of change in density (Margalef 1969; Hurd et al. 1971; Peterson et al. 1993). The critical question here is, How does the degree of omnivory in an ecological assemblage influence its recovery from an experimental perturbation?

The keys to my experiment are the concurrent manipulation of different trophic levels and testing for a possible interaction between the degree of omnivory in an assemblage and its response to a short-term perturbation of prey abundance. A statistically significant interaction term indicates one of two possibilities. If an elevated degree of omnivory exaggerates the community response to the perturbation, then omnivory is functioning as a destabilizing factor; conversely, if elevated levels of omnivory lessen the community response to the perturbation, then omnivory is acting as a stabilizing force.

<div align="center">EXPERIMENTAL METHODOLOGY</div>

I conducted experiments in the ''blowdown zone'' of Mount Saint Helens National Volcanic Monument, Washington. Since the devastating 1980 eruption of Mount Saint Helens, two early successional plants, fireweed (*Epilobium angustifolium*) and pearly everlasting (*Anaphalis margaritacea*), have dominated the blowdown zone landscape (Del Moral and Bliss 1993). In an otherwise inhospitable pumice and ash terrain, these clonal plants form naturally isolated patches of vegetation and detritus that accumulate persistent arthropod assemblages (e.g., Morris et al. 1992; Ives et al. 1993).

Plot Construction and Statistical Design

On July 27, 1994, field assistants and I constructed 30 2.25-m^2 field plots using rigid plastic garden edging (15 cm high) to enclose single discrete patches of *Epilobium* and *Anaphalis.* To prevent dispersal by ground arthropods, I sank the edging 5 cm deep into the ashy soil (which solidifies quickly following disruption) and painted both faces of the exposed portion of the edging with fluon, a slippery industrial lubricant (Wiles and Jepson 1992). These entrenched dispersal barriers maintained densities of manipulated species but did not generate artifactual microclimatic changes that are often a problem with full cage enclosures.

In a balanced two-way factorial design, I crossed three omnivory levels with two levels of a pesticide perturbation designed to induce changes in (i.e., destabilize) the dynamics of the arthropod assemblage. I assigned each of the 30 plots to one of the six resulting treatments.

Omnivory Manipulations

Wolf spiders (*Pardosa mackenziana* and *Pardosa wyuta*) are abundant omnivores in the blowdown zone that feed on numerous arthropod species from multiple trophic levels including herbivores, detritivores, predators, and other
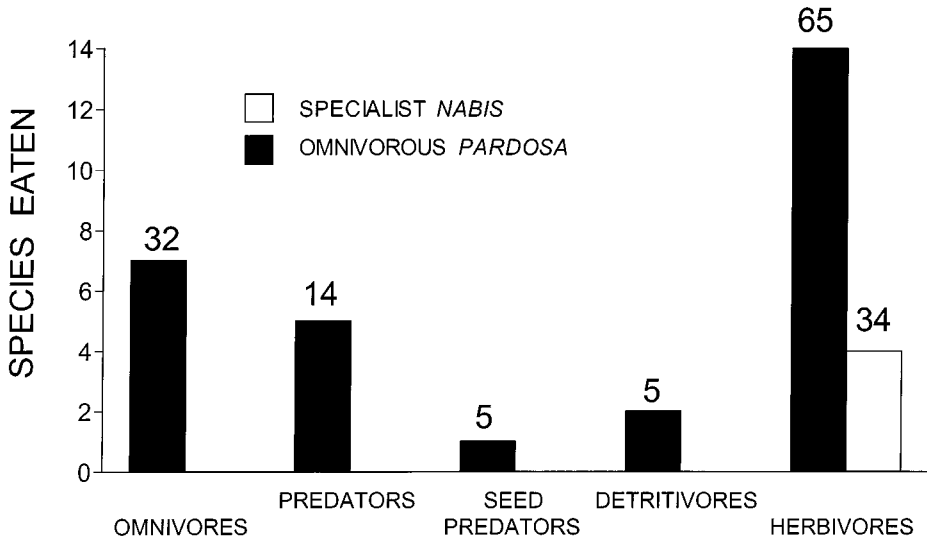
FIG. 1.—Contrasting prey distributions for omnivorous wolf spiders *Pardosa mackenziana* and *Pardosa wyuta* and a more specialized predator (*Nabis alternatus uniformis,* a non-omnivorous damselbug). Data are from direct, unmanipulated feeding observations witnessed during 1993–1995 in the blowdown zone at Mount Saint Helens. To acquire these data, field assistants and I followed free-roaming *Pardosa* and *Nabis* at a distance for fixed periods of time, noting movement patterns, encounters with other free-roaming arthropods, and feeding activities (W. F. Fagan, unpublished manuscript). The open landscape of the blowdown zone and the stark contrast between moving arthropods and pumice and ash substrates facilitate collection of such observational data. Number of observations are above the bars. In a food web context, omnivory has a broad definition: organisms that feed on predators and herbivores are omnivorous, as are organisms that feed on both herbivores and vegetation.

omnivores (fig. 1). In contrast, *Nabis alternatus uniformis* is a nonomnivorous damselbug that specializes on a select group of herbivore prey species including aphids (fig. 1). A simplified food web (fig. 2) depicts feeding linkages among the blowdown zone arthropods included in this study. By altering the relative densities of these omnivores and specialist predators, I manipulated the degree of omnivory in field plots. On August 1, 1994, I removed all resident *Nabis* ($\overline{X}$ [$\pm$ 95% confidence interval (CI)] = 2.4 [$\pm$ 0.7] damselbugs plot^{-1}) and added four *Pardosa* to each of 10 plots to increase the degree of omnivory. In 10 other plots, I removed all resident *Pardosa* ($\overline{X}$ [$\pm$ CI] = 3.1 [$\pm$ 1.1] spiders plot^{-1}) and added four *Nabis* to decrease the degree of omnivory (i.e., to increase the degree of specialization). I censused, but did not manipulate, *Pardosa* and *Nabis* in the remaining 10 plots, which served as controls. Note that, as a result of my manipulations, total predator density varied among plots, albeit slightly. I accounted for such deviations in total predator density in my statistical analyses (see below). Nevertheless, the key component of these manipulations is a change in relative predator densities: my manipulations shifted the composition of the predator assemblages among treatments.
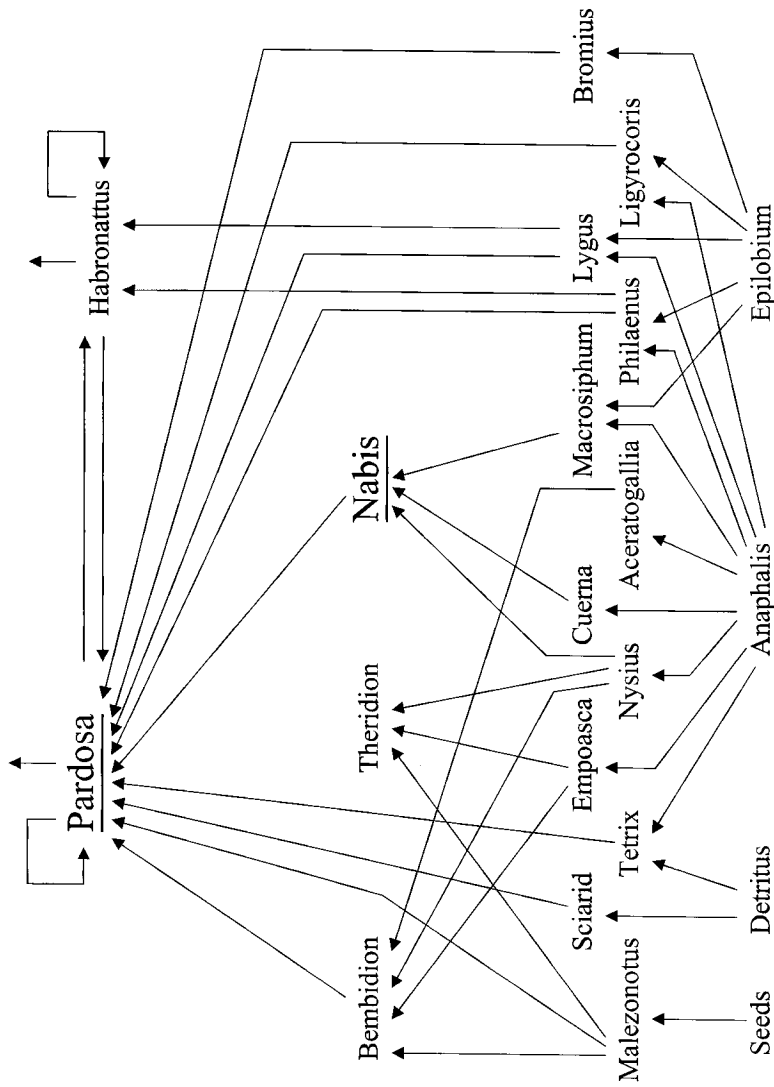
Fig. 2.—Feeding relationships among arthropod species in the Mount Saint Helens blowdown zone. These data compose only a partial food web: only links among this study's focal species are included. All food web links drawn here are based on direct feeding interactions observed under natural, unmanipulated field conditions in the blowdown zone. Detailed species identifications and taxonomic affiliations are given in table 1.

Pesticide Manipulations

For this factor, I destabilized the assemblage in 15 of the 30 plots (five plots at each of the three degrees of omnivory), by selectively reducing the abundance of the aphid *Macrosiphum valeriani. Macrosiphum* is an exceedingly common herbivore at Mount Saint Helens and serves as a principal prey item for *Nabis* (fig. 2). A dramatic reduction in the abundance of this important herbivore species had the potential to affect indirectly many other species in the food web, perhaps leading to shifts in species' abundances among trophic levels (e.g., Diehl 1993; Wootton 1994). I reduced *Macrosiphum* with the short-lived, highly selective aphicide RH-7988 (a butyl-cholinesterase blocker [Rohm and Haas Co., Philadelphia]; Murray et al. 1988), which I applied on July 27, 1994, at a concentration of 1.055 mg L^{-1}.

Data Collection and Analysis

Starting August 15, 1994, I censused all plots by hand biweekly for 6 wk, during the peak of the summer arthropod activity at Mount Saint Helens. Densities and rates of change in densities for the 14 most common and widespread arthropod species at the site served as the response variables in my analyses. I excluded the omnivores, specialists, and aphids whose densities I manipulated and several species of rare and/or patchily distributed arthropods from my analyses of the community's response.

Rather than perform a single, bulky analysis that was multivariate for both species and census times, I extracted from my data a mean density and rate of change in density (i.e., the slope of a regression of abundance against time) for each of the 14 principal species in each of the 30 plots. I then performed two separate MANOVAs: one on mean density (using $\log(N + 1)$ transformations for aphid density and a Freeman-Tukey transformation for all other species) and the other on rate of change in density. In both analyses, the 14 arthropod species served as the multivariate response variables, and per plot total manipulated predator density (i.e., *Pardosa + Nabis,* averaged across time) and per plot plant abundance appeared as additive covariates. Within this statistical design, examining the particular form of interaction effects identifies whether increasing the degree of omnivory had a stabilizing or destabilizing influence. Unlike traditional theoretical stability analyses where stability or instability translates into recovery toward or divergence from some fixed community equilibrium, in this experimental context, I judge (in)stability by comparing dynamics in experimental plots with the seasonal trajectories the community could ordinarily follow.

To quantify further the potential interactions between the degree of omnivory and disturbance, I performed a discriminant function analysis (Manly 1994) on arthropod densities averaged across time within plots. This analysis describes the community's response to the experimental manipulations as orthogonal linear combinations of the component species' responses.

As a final probe into the ecological consequences of my manipulations, I calculated, for each of the 14 species in each plot, the per capita rate of change over the course of the experiment. I then calculated the coefficient of variation

in per capita rates of change among species within plots, including an adjustment to the coefficient of variation formula for small sample sizes (Sokal and Rohlf 1995). This calculated variable provides an estimate of among-species variability in population growth rates after factoring in local differences in density.

<center>RESULTS AND DISCUSSION</center>

The fluon-coated dispersal barriers successfully maintained treatment differences in *Pardosa* and *Nabis* densities throughout the experiment (fig. 3*A, B*). In contrast, the destabilizing reduction in *Macrosiphum* densities was a short-lived pulse (fig. 3*C*); by week 6, aphicide application plots and the no-disturbance controls were statistically indistinguishable in terms of aphid densities.

I found a significant multivariate interaction effect between the omnivory and aphicide factors on mean species' densities (MANOVA: Wilks's λ = 0.039; F = 2.601, df = 28, 18, P = .019). In univariate analyses, the interaction term was significant for seven of the 14 species. In all of these cases, plots with high levels of omnivory had reduced responses to the aphicide disturbance (table 1), results consistent with the hypothesis that omnivory is stabilizing. In contrast to predictions from classical theory, no species exhibited dynamics suggestive of a destabilizing effect of omnivory (table 1).

Of the seven species whose mean densities in the presence of the aphicide perturbation were stabilized by an increased degree of omnivory, five exhibited significant increases in mean density in the aphicide plots with an increased degree of specialization relative to nonaphicide plots (e.g., fig. 4) while two exhibited significant decreases. On average, species densities in aphicide plots dominated by omnivores varied little from comparable nonaphicide plots (average absolute percentage change [$\pm$ CI] = 29 [$\pm$ 12]), whereas their densities in aphicide plots dominated by specialist predators changed radically (average absolute percentage change [$\pm$ CI] = 184 [$\pm$ 127]).

Similarly, I found a significant multivariate interaction effect on rate of change of species' densities (MANOVA: Wilks's λ = 0.027; F = 3.264, df = 28, 18, P = .006). Two herbivorous species, *Aceratogallia* sp. and *Ligyrocoris slyvestris,* exhibited significant univariate interaction effects indicative of enhanced stability with an increased degree of omnivory (fig. 5), and three other species' responses were nearly significant in the same direction. Once again, no species exhibited dynamics suggestive of a destabilizing effect of omnivory.

The discriminant analysis also demonstrated that omnivory stabilized the community effects of the aphicide-induced disturbance (fig. 6). Of all the plots to which I applied aphicide, only those dominated by omnivores fell in the same portion of multivariate space as did the no-aphicide control plots.

Finally, analyses revealed a significant interaction effect for among-species variability in per capita rates of change (fig. 7). Specifically, the aphicide application increased among-species variability in per capita rates of change in plots dominated by specialists but did not significantly affect this measure in plots dominated by omnivores.
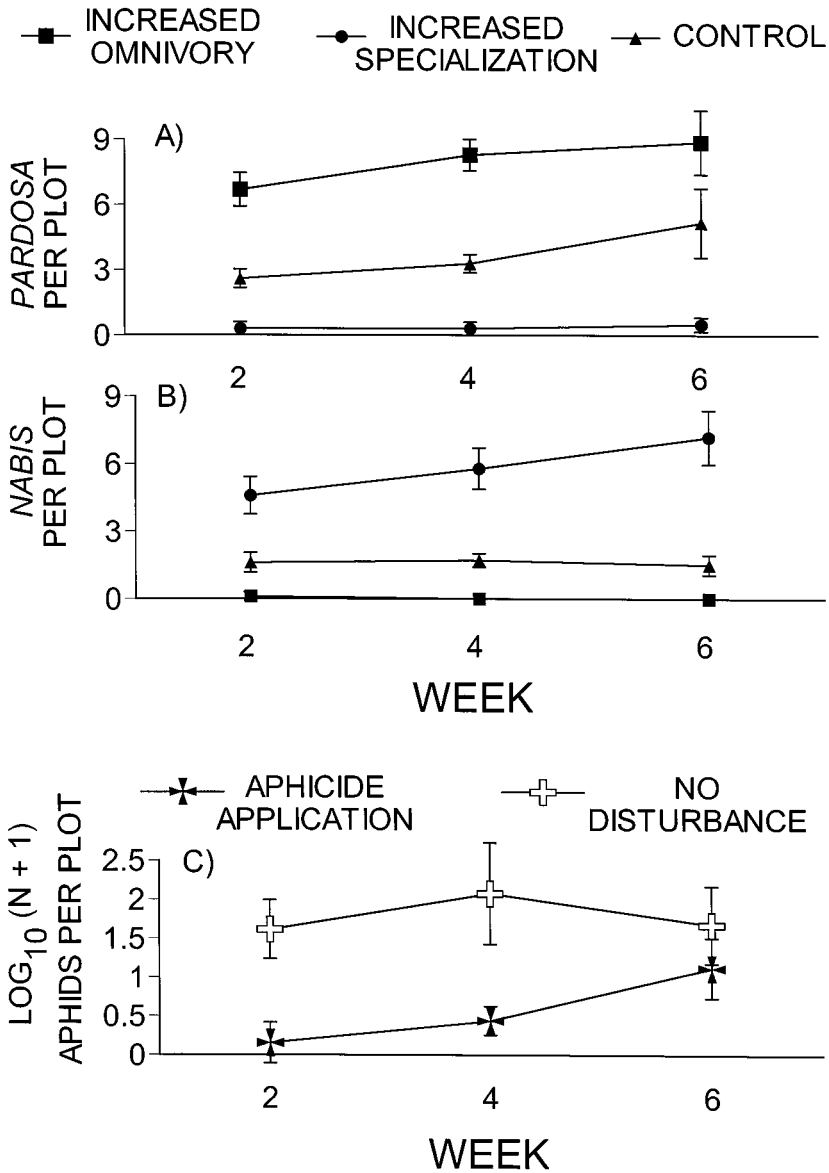
FIG. 3.—Mean (± 95% CI) per plot abundance of (*A*) omnivorous *Pardosa,* (*B*) special-ized *Nabis,* and (*C*) *Macrosiphum* aphids over the course of the experiment. Fluon-coated dispersal barriers successfully maintained among-treatment differences in densities of manip-ulated consumer species (*A, B*). The aphicide application was a short-lived, destabilizing shock to the arthropod assemblage: by week 6, aphid densities in aphicide application plots were statistically indistinguishable from those in the no-disturbance plots (*C*).

TABLE 1

DENSITY RESPONSES OF 14 WIDESPREAD AND COMMON
ARTHROPOD SPECIES AT MOUNT SAINT HELENS TO CONCURRENT
EXPERIMENTAL MANIPULATIONS OF THE DEGREE
OF OMNIVORY AND APHICIDE APPLICATION

Genus and Species Name (Family)	*P*
Species significantly stabilized by increased omnivory:	
Aceratogallia sp. (Cicadellidae)	<.001
Empoasca sp. (Cicadellidae)	<.001
Cuerna sp. (Cicadellidae)	.041
Lygus sp. (Miridae)	<.001
Sciaridae #1	.017
Theridion bimaculatum (Theridiidae)	.003
Bembidion quadrimaculata (Carabidae)	.019
Species exhibiting no significant interaction effect:	
Tetrix subulata (Tetrigidae)	.323
Philaenus spumarius (Cercopidae)	.250
Malezonotus arcuatus (Lygaeidae)	.440
Ligyrocoris sylvestris (Lygaeidae)	.302
Nysius sp. (Lygaeidae)	.471
Bromius obscurus (Chrysomelidae)	.667
Habronattus hirsutus (Salticidae)	.560
Species significantly destabilized by omnivory:	
None	. . .

NOTE.—*P* values from univariate *F*-tests for significant interaction effects between omnivory and aphicide factors conducted as part of the overall MANOVA on arthropod densities. Feeding relationships among these species are presented in figure 2.

Several lines of analysis thus suggest that increasing the degree of omnivory helped to stabilize rather than destabilize the dynamics of the experimentally disturbed community at Mount Saint Helens. Not only were the specialist predators unable to prevent the large shifts in abundance induced indirectly by the aphicide application, but the specialists' particular trophic linkages and behavioral characteristics appear to have actually exacerbated the pesticide's effects in some instances. For example, behavioral observations (Fagan 1996) indicate that the density of a herbivorous cicadellid (*Cuerna* sp.) decreased dramatically in aphicide plots dominated by specialists because *Nabis* began feeding heavily on *Cuerna* once *Macrosiphum* (another prey of *Nabis;* fig. 2) was reduced by the aphicide treatment. In contrast, predation by the omnivorous spiders was spread more evenly throughout the community (figs. 1, 2) and did not engender such dramatic indirect effects. The omnivores' stabilizing effects on community dynamics extend beyond the single season—single vegetation patch scale of this experiment. I have detected comparable impacts on a two season/multipatch scale and for a range of experimental disturbances (Fagan 1996).

This experiment's results contradict predictions from classical food web theory. Increasing the degree of omnivory had a pronounced stabilizing effect on community dynamics here, whereas traditional theory predicts omnivory to be a strongly destabilizing factor (e.g., Pimm and Lawton 1978). The hypothesis that
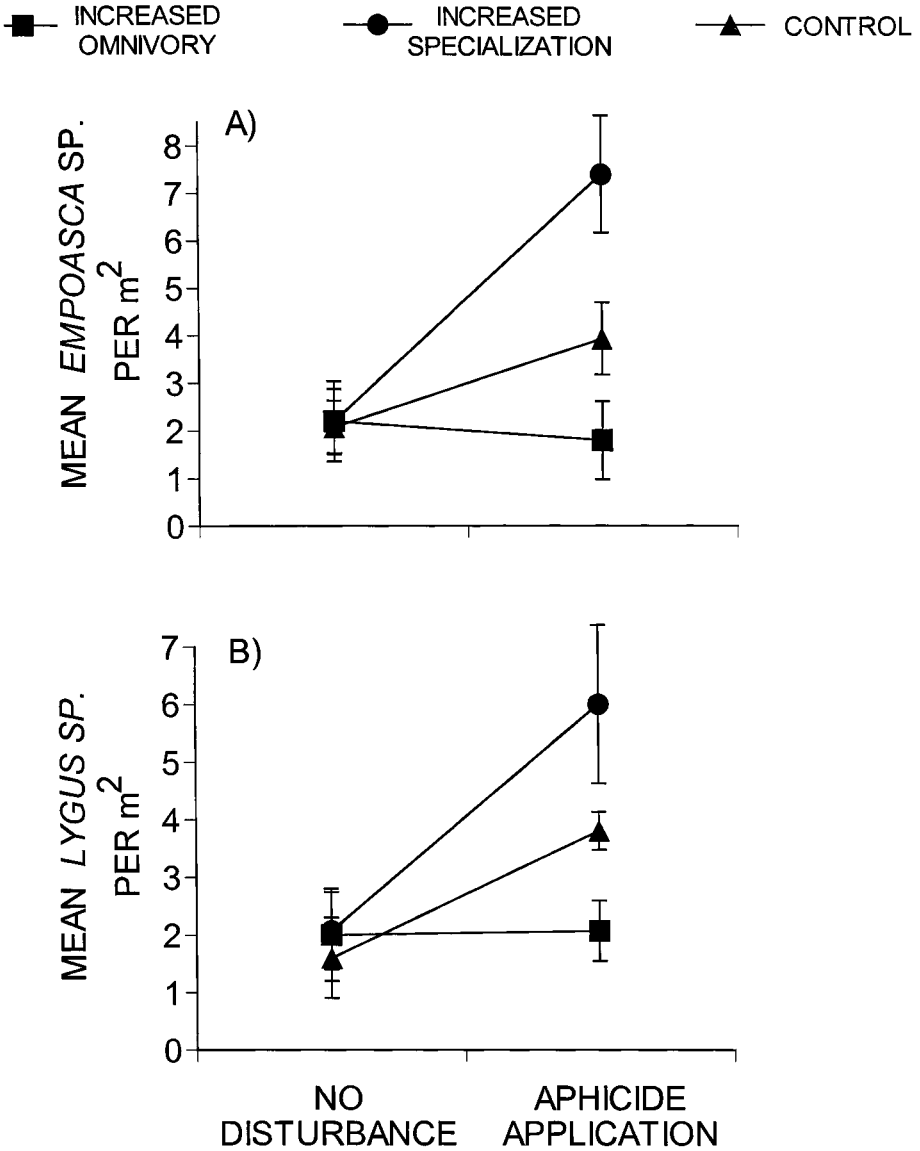
FIG. 4.—Mean (± 95% CI) density of two representative arthropod species at Mount Saint Helens showing interaction effects resulting from concurrent manipulations of degree of omnivory and aphid abundance. A, *Empoasca:* two-way ANOVA, $F = 17.771$, df $= 2, 22$, $P < .001$. B, *Lygus:* two-way ANOVA, $F = 11.886$, df $= 2, 22$, $P < .001$. In plots dominated by omnivores, neither species exhibited a significant change in density across the two disturbance levels, but in plots dominated by specialists, both species exhibited large changes in density across the two disturbance levels. This type of interaction effect indicates that a high degree of omnivory had a stabilizing influence on these species' dynamics.
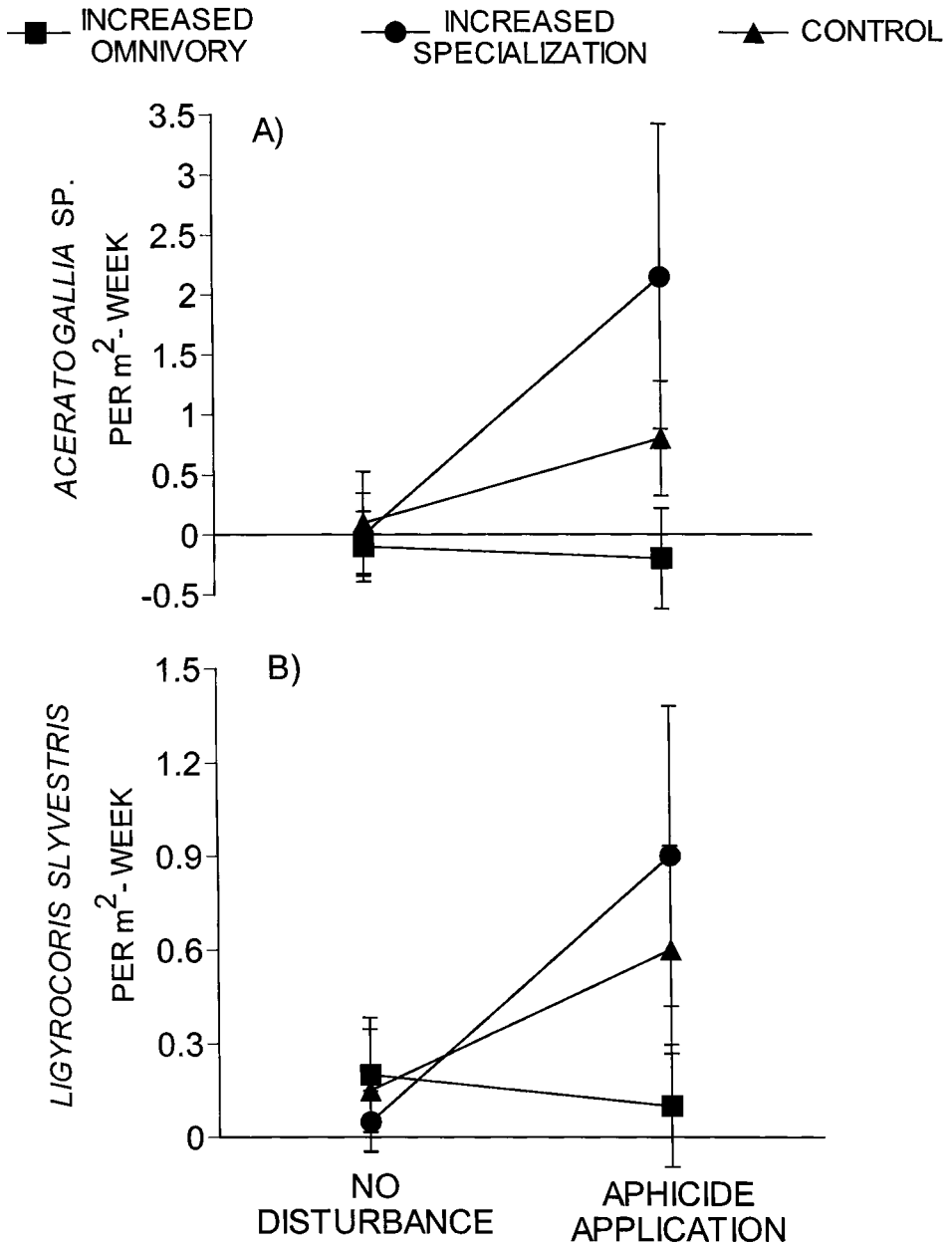
FIG. 5.—Mean ($\pm$ 95% CI) rate of change in density of two arthropod species at Mount Saint Helens. Interaction effects resulting from concurrent manipulations of degree of omnivory and aphid abundance. *A, Aceratogallia:* two-way ANOVA, $F = 4.410$, df $= 2, 22$, $P = .025$. *B, Ligyrocoris:* two-way ANOVA, $F = 4.468$, df $= 2, 22$, $P = .024$.
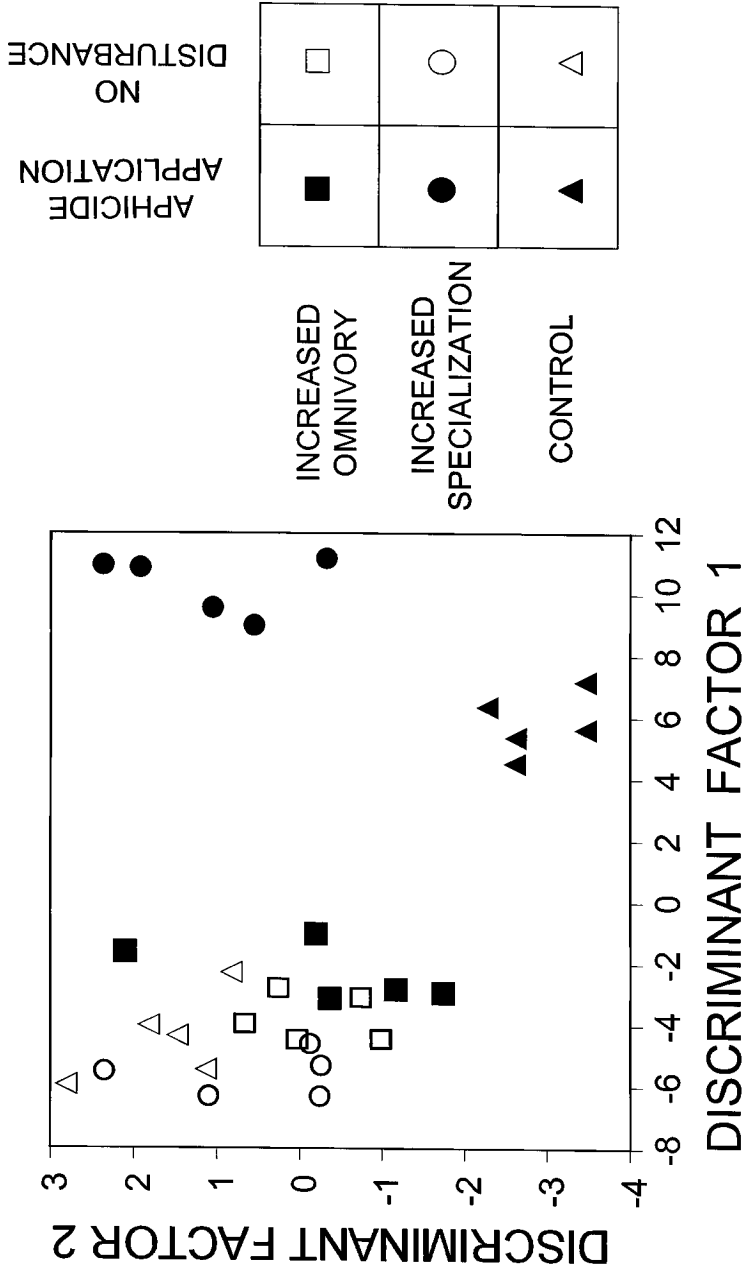
FIG. 6.—Multivariate representation of the Mount Saint Helens arthropod assemblage's response to experimental manipulations of omnivory and aphicide application. Each graphed symbol represents an individual field plot, keyed as in the legend. Using discriminant function analysis, an overall community response to the experimental manipulations can be described as orthogonal linear combinations of the component species' responses (e.g., discriminant factor 1 primarily reflects among-plot differences in herbivore abundances). Clustering of like symbols indicates that experimental treatment combinations had generally similar effects among replicates. On a multivariate level, aphicide plots dominated by specialists and aphicide plots with a control degree of omnivory changed in different ways, reflecting the compositional differences of their predator assemblages. Of all the aphicide plots, only those with a high degree of omnivory fall in the same region of multivariate space as the no-aphicide control plots.
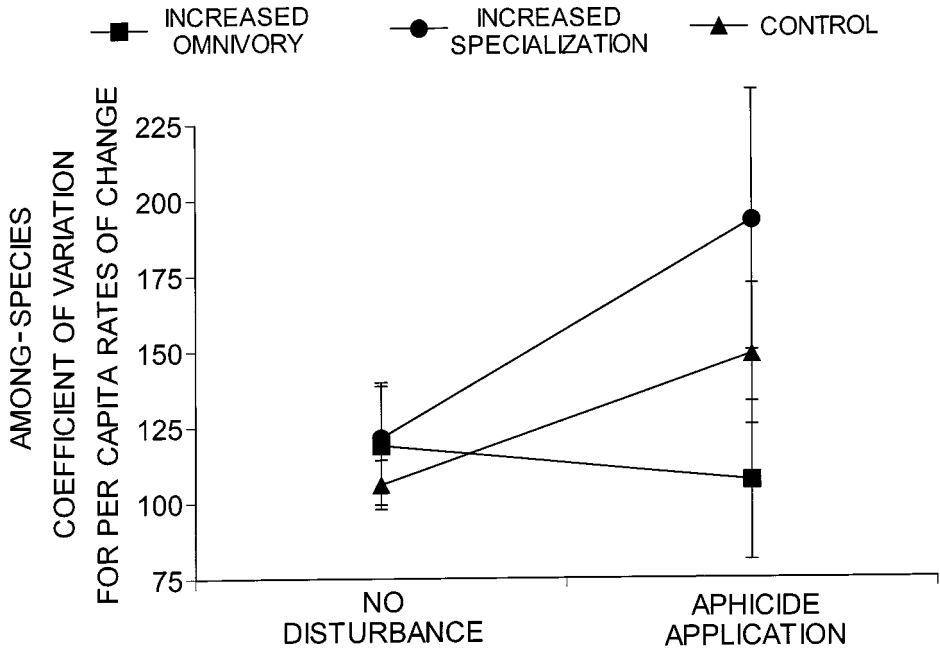
Fig. 7.—Mean ($\pm$ 95% CI) among-species coefficient of variation for per capita rates of change. This calculation provides a measure of among-species variability in population growth rates after factoring in local differences in density. (Two-way ANOVA, $F = 4.958$, df $= 2, 22$, $P = .017$).

omnivory could be a generally stabilizing influence in natural communities is not yet associated with a formal model. However, similar ideas have appeared before in ecology (e.g., MacArthur 1955; Darnell 1961), and the potential stabilizing influences of omnivory are increasingly advocated (Strong 1992; Polis 1994; Polis and Strong 1996) as complex food web architectures are more fully documented (e.g., Winemiller 1990; Polis 1991).

Omnivores, by being directly linked to numerous species on multiple trophic levels, may respond quickly to major community perturbations such as kill-offs or outbreaks of one or a few species, shifting their impacts among species and trophic levels as relative abundances fluctuate and muting the dynamic impacts of perturbations. In contrast, a specialized predator that feeds only on selected species from the next lower trophic level has many fewer options. Faced with a shortfall of a principal prey species, a specialized predator must prey more intensively on one or a few alternative prey, perhaps engendering strong indirect effects that exacerbate the community impacts of the initial disturbance. Similarly a specialized predator must ''wait for'' any increase in productivity to pass up the food web before benefiting from an energy bloom. Such distinctions between omnivores and specialists are crucial because they mean that omnivores can take dynamic shortcuts, quickly tapping into surges or shifts in productivity

by consuming directly from several trophic levels (Sprules and Bowerman 1988; Polis 1991).

Clearly, such a versatile feeding pattern is advantageous to the omnivorous species itself because it offers a measure of risk-spreading (see, e.g., den Boer 1968; Morin and Lawler 1995). But, from the community point of view, an increased degree of omnivory introduces a potential buffering mechanism that may lessen the severity and/or duration of disturbance-induced changes (figs. 4–7).

In a reticulate food web like that of the blowdown zone at Mount Saint Helens, voracious omnivores can influence the composition of a species assemblage through a great diversity of trophic pathways (fig. 2). Such an extensive network of species interactions may allow omnivores to buffer a community from population blooms and compositional shifts induced by both natural and experimental disturbances. Despite a long history of research on the potential for such dynamic buffering in complex communities (e.g., MacArthur 1955; May 1973), the issue deserves additional study from new experimental and theoretical perspectives.

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